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## THE AMERICAN VARIETY OF SAXIFRAGA AIZOON

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(Plate 817)

*Saxifraga Aizoon* Jacq. is the only American representative of the essentially European section *Euaizoonia* (the genus *Chondrosea* of Haworth). According to the treatment of Engler and Irmscher<sup>1</sup>, this section contains 10 species all of which occur in the mountains of central and southern Europe. Eight of the species are confined to more or less restricted areas of this region; *S. Cotyledon* L. occurs also in western and northern Scandinavia and in Iceland, while *S. Aizoon* has a truly remarkable range: all the central European mountains from the Pyrenees to the Carpathians; southward to Corsica, in the Apennines to the latitude of Naples, and to the mountains of northern and central Greece; eastward to Asia Minor, Armenia and (as the subspecies *cartilaginea*) to the Caucasus; two restricted districts in Scandinavia<sup>2</sup>; Iceland<sup>3</sup>; East Greenland to latitude 71° 20' N., West

<sup>1</sup> Das Pflanzenreich, IV, 117 (1919).

<sup>2</sup> *S. Aizoon* is very rare in Scandinavia, occurring only in two widely separated districts: 1. the Ryfylke east of Stavanger in southeastern Norway in latitude 59° 25'; 2. in the mountains east of Saltdal in latitude 67°, where it occurs on both sides of the boundary between Norway and Sweden. There is a considerable Scandinavian literature in reference to this plant, from the standpoint both of its taxonomy and its plant-geography. See Neuman, L. M. Bidrag till Kännedomen af floran vid Saltenfjord och på Sulitälmaområdet i Norge. Botaniska Notiser 1905, p. 263, where he described the northern plant as a new subspecies, *S. Aizoon* Jacq. \**Laestadii* L. M. Neuman (a name completely ignored by Engler and Irmscher); Dahl, Ove, Botaniske undersøgelser i indre Ryfylke, Forhandlinger i Videnskabs-selskabet i Christiania 1906, no. 3 (p. 35) and 1907, no. 4. (p. 34), where the occurrence of the more southerly plant is discussed, and a new form is described; Nordhagen, Rolf, Om *Arenaria humifusa* Wg. og dens betydning for utforskningen av Skandinavias eldste floraelement, Bergens Museums Årbok 1935 Naturvidenskapelig rekke Nr. 1 (pp. 125, 135,



Greenland to latitude  $74^{\circ} 31'$ ; Baffin Island to latitude  $73^{\circ}$ ; Newfoundland; and on the continent of North America from northernmost Labrador to northern Vermont and westward to Hudson Bay, the Lake Superior region, and apparently to the Saskatchewan Valley and Great Slave Lake. It does not occur anywhere in the Rocky Mountains or westward.<sup>4</sup>

As early as 1830 this extraordinary range caught the attention of students of phytogeography. Ernst H. F. Meyer makes the following observation: "On account of the singular geographical distribution I had suspected that the American and Icelandic plant differs from the Austrian and Swiss species until a sedulous examination of Greenland specimens taught me the contrary."<sup>5</sup>

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163); Skandinavias fjellflora og den relasjoner till den siste istid, Nordiska (19, skandinaviska) naturforskarmötet i Helsingfors 1936, pp. 93-124.

<sup>3</sup> Engler and Irmscher say, "Auf Island und den Faeröen fehlend." This is certainly erroneous in so far as it concerns Iceland. There is an Icelandic specimen in the Gray Herbarium, and Ostenfeld and Gröntved say in their Flora of Iceland and the Faeroes, "Icel. rare, found in a few places of the N.E. and SW"

<sup>4</sup> I have seen no specimens from west of Lake Superior. It is reported from Shoal Lake, Manitoba (just north of Lake-of-the-Woods) in the Check List of Manitoba Flora, published by the botanical section of the Natural History Society of Manitoba, in 1922. The reports of its occurrence in "Saskatchewan" go back to Hooker's Flora Boreali-Americana and are undoubtedly authentic, though the exact extent of the country covered by this term in 1834 is somewhat doubtful. Its occurrence in the North-west Territories about Great Slave Lake is reported by Nicholas Palunin in his Botany of the Eastern Arctic, Palunin having presumably taken his record from Raup's Phytogeographic Studies in the Athabaska-Great Slave Lake Region.

There is one report of this species from the Canadian Rocky Mountains, quite definitely erroneous. In his *Phytogeographic Studies in the Peace and upper Liard River Regions, Canada* (Contrib. Arnold Arb. 6, 170), H. M. Raup cites without comment an old report by John Macoun of its presence at the foot of Mt. Selwyn, at the west end of Peace River Pass, Macoun's plants, collected on this occasion, were lost. An examination of the original record (*Canadian Geological Survey; Report of Progress 1875-76*) indicates that the origin of this report was probably a *lapsus calami* on Macoun's part. On p. 146 of the report, in his account of the climb of Mt. Selwyn, he speaks of stopping at the banks of a stream at the foot of the mountain and collecting "Saxifraga oppositifolia, rivularis and Aizoon" and a half dozen other plants. This is the only mention of *S. Aizoon*. It does not appear on p. 148 in the systematic list of the plants collected on Mt. Selwyn (all the other plants mentioned on p. 146 are in this list), nor is it included in the long appendix (pp. 186-232) which includes all the plants collected by him "in the summers of 1872 and 1875 in the Saskatchewan country and on the Peace River, also on the Rocky Mountains in British Columbia and Vancouver Island." Furthermore he does not include this locality for *S. Aizoon* in his *Catalogue of Canadian Plants* published seven years later. It appears almost certain that in the single place where "Aizoon" occurs it was written by mistake for "aizoides", a species which appears in all the above mentioned lists, and which might well occur in the sort of place he is describing.

<sup>5</sup> Meyer, Ernesti, De Plantis Labradoricis Libri Tres. Leipsig. 1830. Quam ob singularem distributionem geographicam plantam Americanam atque Islandicam ab Austriaca atque Helvetica specie differre suspicatus eram, donec specimina Groenlandica sedulo examinata contrariam me docuerunt.



Four years later W. J. Hooker<sup>6</sup> states: "The [American] specimens differ in no respect from those of Europe". Following such categorical statements it has been customary to regard the American plant as completely identical with the European species or even to identify it with certain European subspecific groups.

The European plant is extremely variable in many respects, so much so that Engler and Irmischer designate the species as a "typus polymorphus" and recognize two subspecies, 18 varieties, 8 subvarieties, and 11 forms, a considerable number of which have at one time or another been described as species. They say "hujus typi polymorphi varietates et formae difficile extricantur", and further that they have found the leaf-form and serrature to be the most reliable characters. They identify the American forms with certain central European ones, saying for the plant of Baffin Island "ausschliesslich var. *montana* sub var. *subaffinis*" and for the plants of Greenland and subarctic America, "ausschliesslich var. *montana* subvar. *recta* und subvar. *subaffinis*."<sup>7</sup>

Despite this unanimity of botanical opinion concerning the status of the American plant there are certain small but real differences between it and all the European forms that I have seen. The seeds of the species are about  $\frac{3}{4}$  mm. long, somewhat ridged, and minutely verrucose. The papillae are well seen only under a compound microscope. Those of all European plants examined are crowded, covering all parts of the seed quite uniformly, and when seen in profile appear as steep-sided domes 8–10  $\mu$  high (PLATE 000, FIGS. 4 and 5). The papillae in the American plant are only about half as high, with more gradual slopes, less crowded and on parts of the seed, particularly between the ridges, they may be almost or quite obsolescent (FIGS. 9, 10 and 11). Probably on account of these differences in the papillae, perfectly ripe American seeds often appear somewhat glossy, while the European ones are always dull.

Another difference which appears to be diagnostic is in the

<sup>6</sup> *Flora Bor.-Am.* 1, p. 243 (1834).

<sup>7</sup> Engler & Irmischer, loc. cit. pp. 501 and 502. Their names for these European forms are not in accordance with the International Rules, since the oldest *varietal* name seems to be *S. aizoon*  $\beta$  *recta* Ser. ex D. C. Prodr. iv. p. 19 (1830). At least it antedates their newly coined var. *montana* by 89 years.



configuration of the stomium of the dehisced capsule. In the European plant the edges of the beaks along the line of dehiscence are relatively thick, while outside the opening thus defined are somewhat vague folds. In the American plant, on the other hand, the separating edges of the carpel-beaks are relatively thin, while a thick and definite cord runs down each side of each beak and unites with the corresponding cord of the other beak to form a distinct outer frame about the stomium (Figs. 2, 3, 7, and 8).

Besides these characters, which appear to be entirely consistent, there are a number of tendencies which, while usually giving a characteristic appearance to the American plant, are not sufficiently distinct to separate it sharply from the European. The leaves of well developed plants have much the same shape as in the European var. *recta* but with a little greater tendency to be somewhat cuneiform. However in poorly developed rosettes of normal plants and in the depauperate plants of colder habitats the leaves tend to be obovate-cuneate to nearly elliptic, quite different from the short linguiform leaves of the corresponding European subvar. *subaffinis* and approaching those figured by Engler and Irmscher<sup>8</sup> for var. *typica* subvar. *brevifolia*.

In general the leaves of the American variety seem to be thicker than those of the European ones. In herbarium material of the European plant it is often possible to observe the entire vein-system of a leaf by holding it up in front of a strong light. In no case does this hold for the American plant.

The inflorescence in well developed European plants usually has widely spreading branches which curve upward from an almost divaricate base. In the American plant the branches of the inflorescence are more ascending, and the whole panicle denser in consequence.

In the American plant the cauline leaves tend to be larger and more numerous than in the European. There are a good many exceptions to this, but in looking through large collections of the two, one is struck by the greater leafiness of the American specimens.

There is a strong tendency for the fruiting ovary of the American plant to be better developed above the insertion of the sepals,

<sup>8</sup> Ibid. p. 490.



and for that of the European plant to be better developed below this level. This character differs considerably among the various individuals in a single collection, and again there is considerable overlapping. All attempts to reduce it to a mathematical formula have broken down, chiefly through difficulties in getting comparable measures of the beaks of the carpels. These differ so much from plant to plant in degree of curvature, amount of splitting on dehiscence, and length of styles and stigmas that it has proved impossible to find any datum-plane that does not introduce too large errors of measurement. The base of the fruit also is often rather indefinite, particularly in the American plant. Despite these difficulties, it is evident on examining a large number of American plants, that the top of the fruiting ovary usually overtops the sepals rather conspicuously, while in the European plant it is generally pretty much concealed by them.

In view of these tendencies, and the two diagnostic characters of fruit and seed it seems that the American plant should be considered as a variety distinct from all the European varieties, which I am calling var. **neogaea**<sup>9</sup>. All the American specimens examined belong to this variety, also all those from Greenland, and the single specimen seen from Iceland. Unfortunately no Scandinavian specimens have been seen, and it is impossible to say whether the plants of Scandinavia are most closely related to the New World variety or to the plants of southern and central Europe<sup>10</sup>.

<sup>9</sup> *SAXIFRAGA AIZOON* Jacq. var. **neogaea**, var. nov. Var. *rectae* Ser. ex D. C. (var. *montanae* Eng. & Irmsch.) similis sed seminibus laevioribus papillis minus altis et minus crebris, fructuum partibus superioribus exsertis, stomiis margine tenui restibusque lateralibus prominentibus instructis. TYPE (in herb. Minn.), *Butters, Burns and Hendrikson* no 52, cliff south of Mountain Lake, Cook Co., Minnesota.

<sup>10</sup> The plants from the two Scandinavian localities are not alike, and Nordhagen has shown that the differences are genetic, by growing them in pots side by side (see photograph in his 1936 paper, p. 107). The northern form (subsp. *Laestadii* Neum.) is described as very dwarf, with elliptic or obovate basal leaves and almost capitate cymes (the axis of the inflorescence 0–5 mm. long, the pedicels equalling the flowers or shorter). The petals are described as yellowish, with rose-colored dots, erect or semi-erect in anthesis. Nothing like this appears to occur in America. The southern form is larger but quite variable in stature, the flowers flat and varying from greenish yellow to milk-white with red dots and stripes. It is said to be intermediate between subsp. *Laestadii* and the central European forms. Nothing is said concerning the fruits and seeds of either form.

Nordhagen is convinced that the northern station represents a survival through the last glacial period a little to the west of its present locality. Concerning the southern station he is uncertain whether the plant is a relic or whether it represents an invasion from Denmark or the "North Sea Continent" at the close of the last glaciation.



As is the case with several of the European varieties, var. *neogaea* occurs in two confluent forms. In the southern part of its range, and occasionally even in the far north the usual form has the leaves of the mature rosettes linguiform and 1.5–4.5 cm. long, the flowering shoots (7–) 10–30 (–45) cm. tall and the many-flowered inflorescence paniculately branched. This I regard as typical var. *neogaea*.

On the other hand, in the colder parts of its range there is a form with obovate-elliptic basal leaves 7–12 mm. long, flowering branches only 2–12 cm. high, and the inflorescence few-flowered and short, sometimes nearly capitate. There are no differences in flowers, fruits or seeds.

The extremes of these two forms are very different in appearance, but they pass into one another by insensible gradations, and leaf-form and inflorescence-height do not entirely correlate. Moreover the same small, rounded leaves are sometimes seen in young rosettes of the tall form, and occasional depauperate individuals closely simulating the dwarf northern plant occur along with the normal form even at the southern limit of its range. The two forms are probably purely ecological, and their geographical distribution merely an expression of the climatic differences in the habitats, but it is possible that, as in the case of the two Norwegian forms, culture under similar conditions would disclose some real genetic differences. Engler and Irmischer treat similar pairs of European forms as subvarieties. However until the dwarf form can be proved to be more than an ecological response to a cold climate and unfavorable growing conditions it seems better to treat it as a form<sup>11</sup>.

All specimens seen from Vermont, the Lake Superior region, and Canada south of the St. Lawrence River belong to typical var. *neogaea*, though occasional depauperate individuals occur in several of the collections. From farther north, the following may be considered typical var. *neogaea* or at least as containing some quite typical individuals<sup>12</sup>. NORTHERN QUEBEC: Ile St.

<sup>11</sup> SAXIFRAGA AIZOON Jacq. var. NEOGAEA forma *frigida*, forma nov., foliis rosularum ellipticis vel obovato-spathulatis 7–12 mm. longis, caulibus 2–12 cm. altis, inflorescentia brevi corymbosa pauciflora. TYPE (in herb. Minn.) E. C. and Lucy B. Abbe and J. Marr. 3860. Hill at Boat Opening, Manitounuk Sound, Quebec.

<sup>12</sup> In these northern collections there are more depauperate individuals than in collections from farther south, and in ample collections there is usually a complete gradient from the largest, typical specimens down to dwarf individuals which must be considered as forma *frigida*. As an example may be cited the collection from Beach



Genevieve, Mingan Islands *Ff. Marie-Victorin et Rolland-Germain* 18793 (G)<sup>13</sup>; calcareous tableland east of Blanc Sablon, *Fernald and Wiegand* 3524 (G); Beach Creek, Richmond Gulf, *Abbe and Abbe* 3249; Old Factory River, *W. G. C. Todd* Aug. 3, 1912 (P). NORTHWEST TERRITORY: Tukarak Island, Belcher Islands, Hudson Bay, *Abbe, Abbe, and Marr*, 4008. NEWFOUNDLAND: Tilt Cove, Northern Shores of Notre Dame Bay, *Fernald and Wiegand* 5520 (G). LABRADOR: September Harbor, *Harlow Bishop* 354 (G). GREENLAND: Neria (61° 30' N.) *I. Eugenius*, Sept. 2, 1925, July 31, 1926 (G); Disko, Godhavn (69° 14' N.) *A. E. Porsild*, Sept. 10–20, 1922 (G); Amitsuatsiaq Fjord (70° 45' N.) *M. P. & R. T. Porsild* July 10, 1929 (G) (the tallest plant 23 cm. high); Uniarfik Fjord (71° 56' N.) *M. P. Porsild*, Sept. 7, 1934 (G).

The following collections may be cited as *S. Aizoon* var. *neogaea* f. *frigida*. NORTHERN QUEBEC: Baie des Moutons, *H. St. John* 90509 (G); Blanc Sablon, *M. T. Doult* June 25, 1939 (P); Great Whale River, *E. C. & Lucy B. Abbe* 3934; Boat Opening, *Abbe, Abbe and Marr* 3860; Port Harrison, *Mrs. G. K. Tallman*, Aug. 7, 1936. NORTHWEST TERRITORY: South Twin Island, James Bay, *M. T. Doult* 2292 & 2347 (P); Goose Id., Belcher Ids., *J. K. Doult* 218 (P); Tukarak Id., Belcher Ids., *J. K. Doult* 209 & 309 (P). LABRADOR: Cape Mugford, *W. E. C. Todd*, Aug. 2, 1920 (P); 20 mi. north of Nakvak, *H. S. Forbes*, Aug. 28, 1908 (G); Rama, *J. D. Sornborger* 37. NEWFOUNDLAND: Fishing Head, St. Anthony, *E. C. Abbe* 425; Chimney Cove, *A. C. Waghorne*. BAFFIN ISLAND: Lake Harbour, *M. O. Malte* 121037 (G); *N. Palunin* 429 (G); Griffen Bay, *David Potter* 8104 (G). GREENLAND: Disko (69° 15' N.) *Aa. Jensen*, 25 July 1936 (G); Safiorfik (72° 23' N.), *Ussing*, 22 July, 1886 (G). ICELAND: Hrethavatn, *Edith Scamman* 1407 (G).

That *Saxifraga Aizoon* originated in the mountains of southern or central Europe seems certain in view of the large number of related species in that region, and also the great variability of *S. Aizoon* itself there. The North American population must have reached this continent by a trans-Atlantic route, presumably by way of Scandinavia, Iceland and Greenland. At least,

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Creek, Richmond Gulf, *E. C. and Lucy B. Abbe* no. 3249. This collection contains 44 flowering specimens. The flowering shoots range from 6.5–21 cm. in height, forming an unbroken series between these extremes. The leaves also vary continuously from elongated linguiform in the large specimens to short-elliptic in the smallest ones. The largest specimens are typical var. *neogaea*, the smallest forma *frigida*.

<sup>13</sup> Through the kindness of the Curators of the Gray Herbarium and of the Herbarium of the Carnegie Museum, Pittsburgh, I have been able to examine a large number of sheets from these institutions. In the following list they are indicated with (G) and (P) respectively; those in the Herbarium of the University of Minnesota are not marked.



if it traversed the British Isles and the Faroes all traces of its presence there were obliterated by the last glacial advance. Its wide distribution in northeastern North America implies a fairly early arrival in the western hemisphere, certainly not later than some of the mid-Pleistocene interglacial periods. On the other hand, a Tertiary invasion seems unlikely in view of its failure to reach the Cordilleran region, or the Canadian West-Arctic. The stock that reached North America must have been genetically pretty uniform since one of the remarkable characteristics of the American population is its uniformity except in such characters as are directly correlated with more or less favorable habitats. This uniformity of the American population argues in favor of an interglacial, rather than a Tertiary invasion of North America, as, in a species which is so extremely variable in Europe, some mutation and division into geographical races would be expected in North America if the plant had been resident here during the whole of the Pleistocene.

The species probably survived the Wisconsin glaciation in numerous refuges. It is almost ideally adapted for survival on a nunatak-area of even rather limited size. One of its most remarkable characters, moreover, is the vigor and speed with which it has occupied suitable sites in the center of the glaciated tract, far from any possible center of survival. Its occurrence on the islands in Hudson Bay is a striking example, for these islands were not only heavily glaciated, but for an indeterminate time after the Wisconsin glaciation they were submerged by the waters of the Bay. In this respect the behavior of the species in North America is in sharp contrast to its behavior in Scandinavia.

In northeastern Minnesota it occurs quite abundantly in Cook Co., on north-facing slate cliffs in a region where the Wisconsin glaciation was apparently confined to valley glaciers pushing into the upland from the main ice-lobe in the Lake Superior basin. One can see no reason why it may not have continued *in situ* since the last interglacial period.

#### EXPLANATION OF PLATE 817

FIGS. 1-5, *SAXIFRAGA AIZOON*, var. *RECTA* from "Transsilvania occidentalis. Biharia. in montibus ad Vidram", *Simkovic's Fl. Exsicc. Austro-Hungarica*, No. 1290 (distributed as *S. robusta* Schott, Nyman et Kotschy, cited by Engler and Irmscher as *S. Aizoon* var. *montana*): FIG. 1, inflorescence,  $\times \frac{1}{2}$ ;



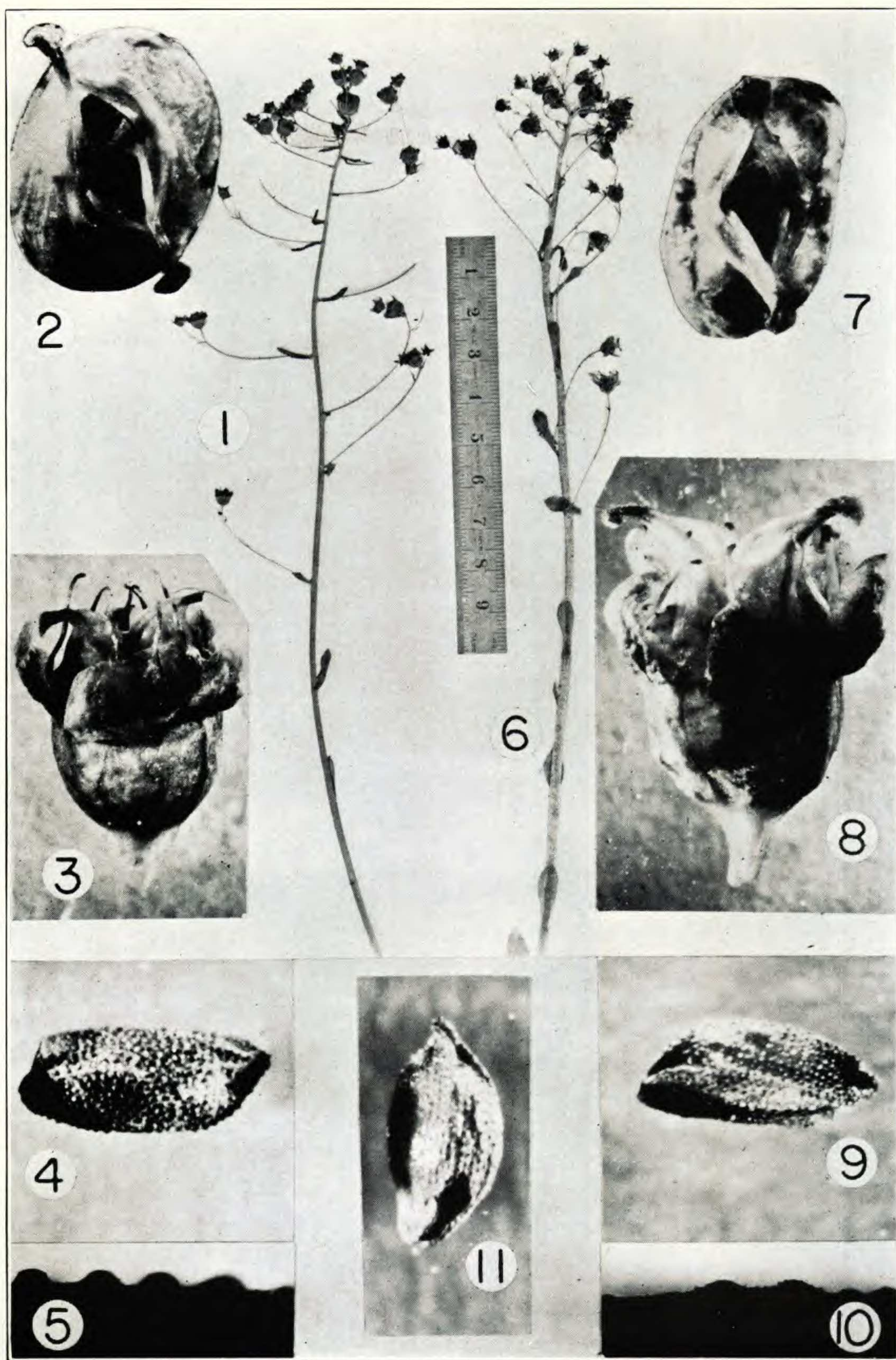


Photo. E. C. Abbe.

SAXIFRAGA AIZOON var. RECTA, from Transsilvania: FIG. 1, inflorescence  $\times \frac{1}{2}$ ; FIG. 2, ripe capsule from above  $\times 8$ ; FIG. 3, ripe capsule from side  $\times 6$ ; FIG. 4, seed  $\times 30$ ; FIG. 5, sculpturing of seeds  $\times 225$ .

Var. NEOGAEA, from TYPE: FIG. 6, inflorescence  $\times \frac{1}{2}$ ; FIG. 7, ripe capsule from above  $\times 8$ ; FIG. 8, ripe capsule from side  $\times 6$ ; FIG. 9, seed  $\times 30$ ; FIG. 10, sculpturing of seed  $\times 225$ .

Var. NEOGAEA f. FRIGIDA: FIG. 11, seed  $\times 30$ , from Great Whale River, Quebec.